Biodiversity, ecosystem function and plant traits in mature and immature plant communities

K. THOMPSON,*† A. P. ASKEW,* J. P. GRIME,* N. P. DUNNETT‡ and
A. J. WILLIS*

*Department of Animal and Plant Sciences and ‡Department of Landscape, University of Sheffield, Sheffield S10 2TN, UK

Several studies of synthesized herbaceous plant communities have reported a positive relationship between vascular plant diversity and biomass production (Naeem *et al*. 1994; Tilman *et al*. 2001), and the European BIODEPTH experiment has been one of the most influential in this regard (Hector *et al*. 1999). Much, though not all, of the evidence for this relationship has come from experimental communities established from seed and harvested after only a year or two. It is not clear that such immature plant communities would be expected to provide reliable evidence of the relationship between diversity and ecosystem properties. Here we compare the relationship between diversity and biomass in BIODEPTH with that at the long-term monitoring site at Bibury in Gloucestershire, UK (Dunnett *et al*. 1998), a natural plant community that has much in common with BIODEPTH. The Bibury site offers a rare opportunity to address questions similar to those tackled by BIODEPTH, while avoiding some of the limitations of short-term experiments.

If a positive relationship between vascular plant diversity and biomass production is an important phenomenon, one could argue that it should be detectable in natural vegetation. Previous attempts to explore the relationship between biodiversity and productivity in natural plant communities have been criticized on the grounds that both variables are frequently affected by additional (usually abiotic) variables (Lawton *et al*. 1998). For example, over a wide range of moderate-to-high biomass values, there is a well known negative relationship between biomass and species richness, driven by increasing competitive exclusion at higher productivity (Grime 1973; Grace 1999; Stevens *et al*. 2004). In experiments such as BIODEPTH, one aim is to exclude such natural sources of variation and create synthesized plant assemblages that vary only in artificially imposed levels of species richness. Of course, random environmental heterogeneity cannot be completely excluded, and Huston & McBride (2002) have shown how such heterogeneity can give rise to spurious diversity–function relationships. However, synthesized communities may also exhibit systematic variation in productivity equalling or exceeding that occurring in natural habitats, arising from the higher nitrogen availability in communities sown with N-fixing legumes. In BIODEPTH, addition of *Trifolium pratense* (nomenclature follows Stace 1997) increased biomass, on average, by 360 g m^{-2} (Hector *et al*. 1999). As this increase was much larger than the effect of any other species, it is reasonable to attribute this effect to a direct result of the extra N fixed by *Trifolium*. The increase was also much larger than the effect of a change in diversity itself; doubling species richness increased biomass, on average, by only 80 g m^{-2}.

The Bibury road verge lies on the north side of Akeman Street, originally a Roman road, in Gloucestershire, UK (National Grid reference SP 119048). The 700 m length of experimental verge was originally chosen because of its considerable width (3·3–5·5 m), uniform vegetation, and the light traffic borne by the accompanying road. The mature vegetation at Bibury has experienced the same management and maintained a very similar species composition over 46 years of monitoring; the biomass and species richness of vascular plants are therefore likely to be at or near equilibrium. Underlying geology is Oolitic limestone, soil pH varies from 7·5 to 7·9, and mean annual rainfall is ≈760 mm. Management consists of a single cut at a height of ≈0·7 m annually in November The vegetation is typical *Arrhenatheretum* (NVC MG1: Rodwell 1992). Over 100 species have been recorded from the site, but only 42 flowering plants were found in this quadrat study. Between 40 and 50% of the above-ground biomass consists of two large perennial grasses, *Arrhenatherum elatius* and *Dactylis glomerata*, while *Heracleum sphondylium*, *Anthriscus sylvestris* and *Convolvulus arvensis* are the commonest forbs. Since 1958, 20 m lengths of verge have been subjected to experimental spraying with maleic hydrazide or maleic hydrazide +2,4-D, while other 20 m lengths acted as unsprayed controls (Yemm & Willis 1962). All spraying ceased in 1990, and it is now impossible to distinguish treated and control plots in terms of biomass, species richness or composition. In each of 12 sections (six treated and six controls) we harvested all above-ground vegetation and litter from four 0·25 m^2 quadrats in July 2003. All harvested vegetation was sorted to species, oven-dried and weighed. Examination of the data revealed that although 11 of the 12 sections were very uniform in species composition, one control section was both more species-rich and dominated
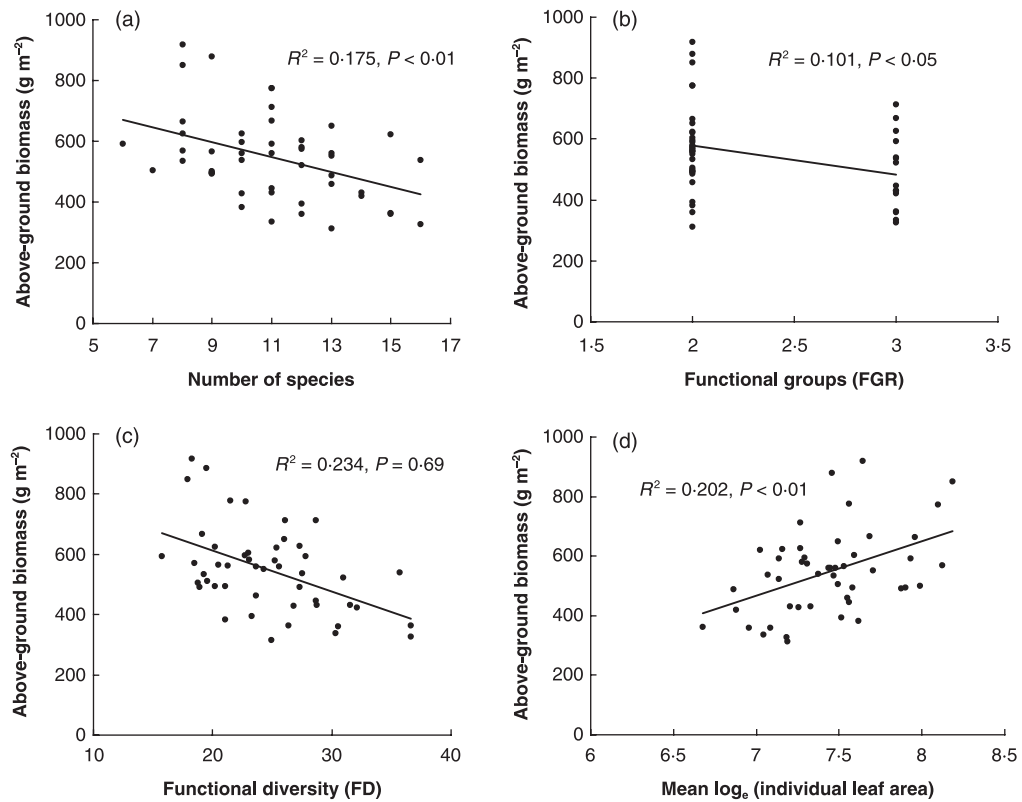
†Author to whom correspondence should be addressed.
E-mail: ken.thompson@sheffield.ac.uk

Fig. 1. Relationship between above-ground biomass in 48 0·25 m^2 quadrats from the Bibury road verge and (a) species richness; (b) functional group richness (FGR); (c) functional diversity (FD); (d) mean log$_e$ individual leaf area (mm^2) of the component species. FGR used three functional groups (legumes, other forbs and grasses), but there are only two levels of FGR as all quadrats contained grasses and forbs. FD with highest r^2 was derived from four traits: legume, leaf area, leaf dry matter content and canopy structure.

by *Festuca arundinacea* and *Festuca rubra* rather than *Arrhenatherum* and *Dactylis*. The analyses presented here are based on all quadrats, but we also analysed (a) all sections except the unusual control section; (b) controls only; and (c) previously sprayed sections only. In each case the results were qualitatively identical.

Although the vegetation at Bibury is notably uniform, local variation in productivity (probably owing to differences in soil depth) is of the same order as the effect of adding legumes to BIODEPTH (mean difference in biomass between the least and most diverse quadrats at Bibury = 246 g m^{-2}). The Bibury vegetation is also very similar in other respects to that at the six northern BIODEPTH sites (Hector *et al*. 1999). Mean biomass at Bibury (553 g m^{-2}) is close to the mean of the six BIODEPTH sites (656 g m^{-2}), and of the 42 species recorded in the Bibury quadrats, 23 (including seven of the 10 most frequent) were also sown in one or more BIODEPTH communities. The range of species richness at Bibury, which was free to vary naturally, was much less than in BIODEPTH (6–16 vs. 1–32 spp.).

From the Bibury quadrat data we examined the relationship between quadrat biomass and three measures of diversity: species richness, functional group richness (FGR) and functional diversity (FD). We also examined the relationship between biomass and mean plant trait values for each quadrat.

For each quadrat, FD was calculated according to a published protocol (Petchey & Gaston 2002; Petchey *et al*. 2004). We used nine candidate traits: specific leaf area; individual leaf area; leaf thickness; leaf dry matter content; seed weight (continuous variables); canopy structure; canopy height; lateral spread (ordered categorical variables, see Grime *et al*. 1988 for details); and legume or not (binary variable). Data were derived largely from an unpublished database (Knevel *et al*. 2003). We calculated FD for each of the 2^9 possible combinations for all quadrats, then tested the predictive power of each candidate measure by linear regression against biomass. This allowed the data themselves to arrive at an objective decision about the functional importance of each trait or combination of traits. Before analysis, all candidate traits were standardized to have a mean of 0 and variance of 1. In addition, those continuous traits that did not meet the assumptions of the ANOVA were previously log or square-root transformed as necessary, although the results were qualitatively identical if this transformation was omitted. The FD values from all 2^9 possible combinations of traits were regressed against biomass, and the highest value of r^2 is plotted in Fig. 1(c). The significance of the relationship in Fig. 1(c) was determined by a bootstrap procedure in which trait values were randomized among species and within traits, then the maximum explanatory power

of FD was calculated for the randomized trait matrix. Repeating this 1000 times produced a bootstrapped distribution of maximum explanatory powers for each measure of FD, against which the observed maximum explanatory power could be compared for statistical significance. We also tested species richness and FGR as predictors of biomass. We used legumes, grasses and forbs as groups (Tilman *et al*. 1997; Hooper 1998), but as all plots contained forbs and grasses, there were only two levels of FGR (+ and – legumes).

We also calculated the mean value of the same nine traits for each quadrat. These values could have been weighted by species abundance, but in order to be strictly comparable with species richness and FD (which cannot easily be weighted), we did not do so. All mean candidate traits, after log or square-root transformation as necessary, were submitted to a stepwise multiple regression with biomass as dependent variable, $P = 0.05$ for entry and $P = 0.1$ for removal. This procedure produced a regression with a single significant variable (individual leaf area; Fig. 1d). No other variable entered the regression until P for entry was raised to 0.3.

In the BIODEPTH communities, biomass was positively correlated with both species richness and FD (Hector *et al*. 1999; Petchey *et al*. 2004), while at Bibury, biomass is negatively correlated with species richness (Fig. 1a), with FGR (Fig. 1b), and with FD, although not significantly (Fig. 1c). Given that the two communities were similar in composition and exhibited similar internal gradients of productivity, imposed by N availability in BIODEPTH and probably by soil depth at Bibury, why was species richness positively related to biomass in the BIODEPTH experiment, while several measures of diversity are negatively related to biomass at Bibury? To explain this striking discrepancy, it is necessary to examine the causes of variation in productivity and species richness at Bibury. The Bibury road verge is typical of relatively undisturbed, moderate-to-high productivity vegetation throughout Britain and northwest Europe. It lies entirely on the right-hand slope of the widely reported 'hump-back' relationship between species richness and biomass (see Grace 1999; Grime 2001 for recent reviews), where there is typically a negative relationship between these two variables. Such vegetation is dominated by a few large, competitive perennials and biennials, and in the quadrats with highest biomass these competitive dominants are able to exclude most other species (Stevens *et al*. 2004). Where biomass is a little lower, for example over shallower soils, other less-competitive 'subordinate' species (Grime 1998) can persist. These subordinates contribute both to increased species richness and (because they differ in many key respects from the dominants) to increased functional diversity, but have little impact on total biomass (Smith & Knapp 2003). The FD and species richness are closely positively correlated at Bibury ($r^2 = 0.63$, $n = 48$).

Although biomass was unrelated to diversity of plant traits at Bibury, it was not unrelated to the traits them-

selves. Multiple regression of mean traits revealed that a single trait, mean area of an individual leaf, was the best predictor of biomass (Fig. 1d). Mean individual leaf area is correlated with canopy height ($r^2 = 0.44$, $n = 43$), i.e. large plants tend to have large leaves, and if leaf area was omitted from the regression, canopy height entered first instead with $r^2 = 0.16$. Thus traits related to competitive dominance, e.g. leaf area and canopy height (Gaudet & Keddy 1988; Hodgson *et al*. 1999), appear to be the best predictors of community biomass at Bibury.

Why is there high diversity in some BIODEPTH plots under conditions that are associated at Bibury with competitive exclusion? Perhaps the most likely explanation is the extreme immaturity of the BIODEPTH communities, which were established from seed in the spring of 1996 and harvested in summer 1997. Less than two growing seasons is unlikely to be sufficient for the normal processes of competitive exclusion to take place, particularly when the potential dominants themselves had to start from seed. We therefore suggest that immature synthesized communities, in which both species richness and the relative contributions of different species are still rapidly changing, are of limited use in exploring the relationship between biodiversity, plant traits and ecosystem functioning. We further suggest that there is probably no causal relationship between species richness and biomass in the BIODEPTH communities, and that the apparent relationship can be explained adequately by the mechanisms described by Huston & McBride (2002) – the greater probability of diverse plots containing both highly competitive species and N-fixers when N is limiting. Interestingly, this effect also appears to be largely responsible for the apparent positive relationship between diversity and biomass in grasslands at Cedar Creek, MN, USA (Lambers *et al*. 2004).

References

Dunnett, N.P., Willis, A.J., Hunt, R. & Grime, J.P. (1998) A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology* **86**, 610–623.

Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* **334**, 242–243.

Grace, J.B. (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics* **2**, 1–28.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature* **242**, 344–347.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**, 902–910.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*. John Wiley & Sons, Chichester, UK.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology: A Functional Approach to Common British Plants*. Unwin-Hyman, London.

Hector, A., Schmid, B., Beierkuhnlein, C. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. (1999) Allocating C–S–R plant functional types: a soft approach to a hard problem. *Oikos* **85**, 282–296.

Hooper, D.U. (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* **79**, 704–719.

Huston, M.A. & McBride, A.C. (2002) Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. *Biodiversity and Ecosystem Functioning* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 47–60. Oxford University Press, Oxford, UK.

Knevel, I.C., Bekker, R.M., Bakker, J.P. & Kleyer, M. (2003) Life-history traits of the Northwest European flora: the LEDA database. *Journal of Vegetation Science* **14**, 611–614.

Lambers, J.H.R., Harpole, W.S., Tilman, D., Knops, J. & Reich, P.B. (2004) Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands. *Ecology Letters* **7**, 661–668.

Lawton, J.H., Naeem, S., Thompson, L.J., Hector, A. & Crawley, M.J. (1998) Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. *Functional Ecology* **12**, 848–852.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–737.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**, 402–411.

Petchey, O.L., Hector, A. & Gaston, K.J. (2004) How do different measures of functional diversity perform? *Ecology* **85**, 847–857.

Rodwell, J.S., ed. (1992) *British Plant Communities Vol. 3: Grasslands and Montane Communities.* Cambridge University Press, Cambridge, UK.

Smith, M.D. & Knapp, A.K. (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* **6**, 509–517.

Stace, C.A. (1997) *New Flora of the British Isles*, 2nd edn. Cambridge University Press, Cambridge, UK.

Stevens, M.H.H., Bunker, D.E., Schnitzer, S.A. & Carson, W.P. (2004) Establishment limitation reduces species recruitment and species richness as soil resources rise. *Journal of Ecology* **92**, 339–347.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845.

Yemm, E.W. & Willis, A.J. (1962) The effect of maleic hydrazide and 2,4-dichlorophenoxyacetic acid on roadside vegetation. *Weed Research* **2**, 24–40.